Variation in Egg and Larva Production of the Anchovy, *Stolephorus purpureus* Fowler, in Kaneohe Bay, Oahu, during 1950–1952[1]

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INTRODUCTION

A SMALL ANCHOVY known locally as the nehu is the principal baitfish used in Hawaii for catching skipjack (*Katsuwonus pelamis*) by live-bait fishing methods (F. C. June, 1951). This baitfish, which is taken commercially by nightlight methods after dark or by surround net in the daytime, occurs in quantity only in a few localities on Oahu, e.g., Pearl Harbor, Honolulu Harbor, Ala Wai Canal, and Kaneohe Bay, all of which are shallow, relatively turbid, and in part brackish. These bays and inlets appear to support separate populations (Tester and Hiatt, 1952). As the supply of nehu comprising the populations appears to fluctuate both seasonally and annually, it is of interest and importance to investigate the causes. One possible factor, variation in egg and larva production, is dealt with here for one population, that of Kaneohe Bay, over a period of 24 consecutive months in the years 1950, 1951, and 1952.

Pertinent information on the spawning habits of the nehu, nature of the eggs and larvae, and the larval growth rate has been given by Tester and Yamashita (1950), Tester (1951), and Yamashita (Ms.). Briefly, the nehu is a pelagic spawner, spawning takes place (in Kaneohe Bay) mostly from 10:00 P.M. to midnight, the bluntly ovoid eggs hatch within about 24 hours or less, the typically clupeid, filiform larva measures about 2 mm. at hatching and appears to have an initial growth rate of about 1.5 mm. per day. A more detailed description of eggs and larvae, including criteria for identification, is given by Tester (1951: 326–327).

Previous studies on the distribution of nehu eggs and larvae in Kaneohe Bay were conducted by Tester (1951) in 1949 and 1950. In these, four general surveys of horizontal distribution (in September, December, March, and June) were made, together with interim surveys of horizontal and vertical distribution. Among other things it was found that (a) spawning took place in all months which were sampled, and no particular spawning season could be defined from the data, (b) the eggs were present at all depths but with a slightly greater abundance towards the surface, (c) most of the eggs occurred within the southern sector of the bay (Fig. 1), (d) within the southern sector, there appeared to be a consistent peak of abundance of eggs in the vicinity of Stations 4 and 5 (between Coconut Island and Mokapu Peninsula), (e) within the southern sector, the larvae appeared to move in a clockwise direction around the bay as they increased in size. It was recommended that a specific sampling program be undertaken at or near Station 4 to investigate in more detail the temporal distribution of eggs and larvae. The recommended program, cur-

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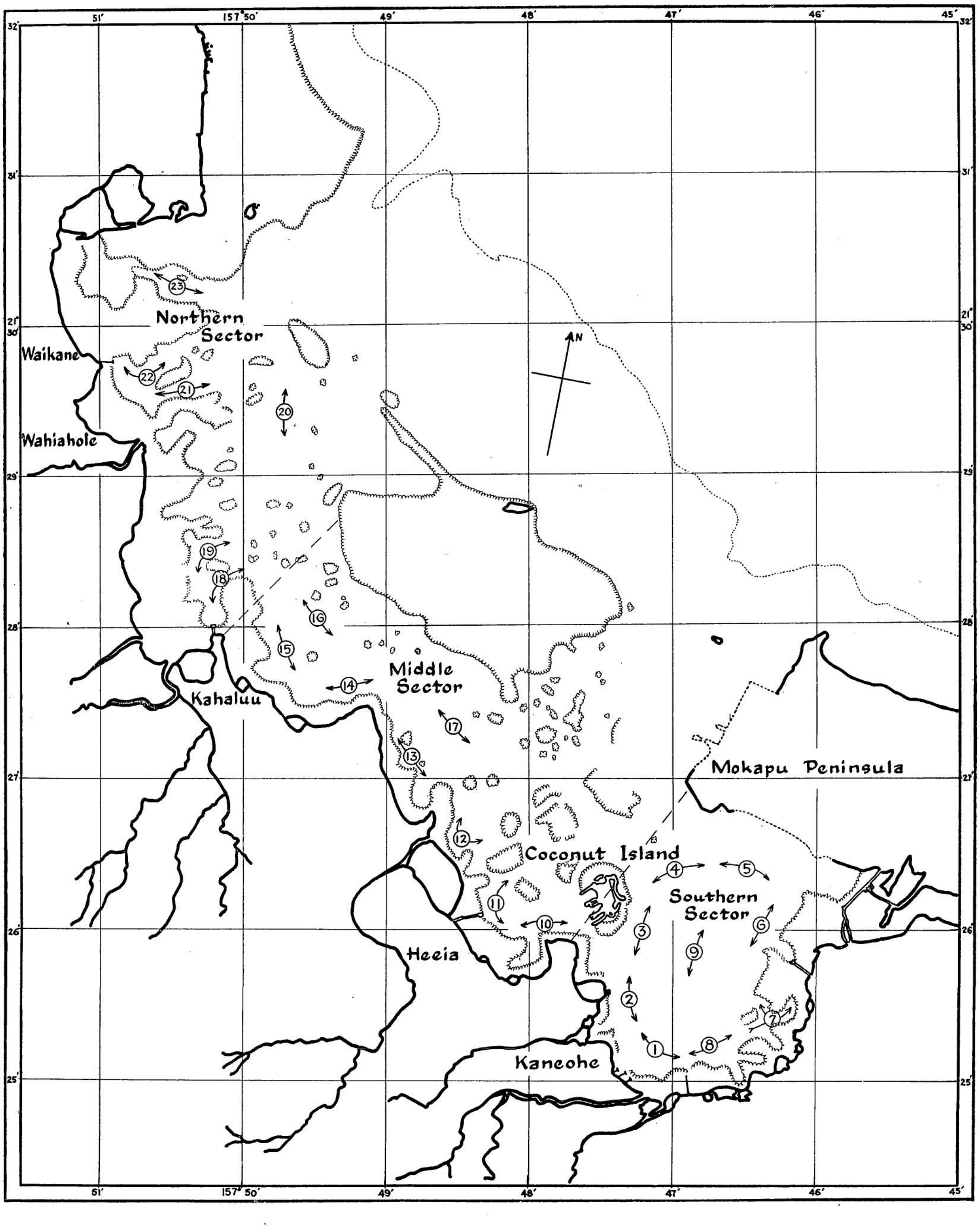

FIG. 1. Map of Kaneohe Bay showing the location of Station 4 (between Coconut Island and Mokapu Peninsula) with respect to the 23 stations sampled in a previous investigation.

tailed in some aspects and expanded in others, was started in 1950 and the data obtained form the basis for the present paper.

Acknowledgments

The investigation could not have been undertaken with efficiency without the specialized knowledge and ever-willing cooperation of Mr. Zukeran, skipper of the University's research vessel "Salpa." He assumed the responsibility of locating the sampling stations and of supervising the sampling procedure. Assistance by several graduate students of the University of Hawaii in field work and particularly in sorting plankton hauls in the laboratory, in counting nehu eggs and larvae, and in measuring fish is also gratefully acknowledged. These included Miss Tetsuko Fujita, Mr. Michio Takata, Mr. Royden Ikeda, and Mr. Austin Pritchard.

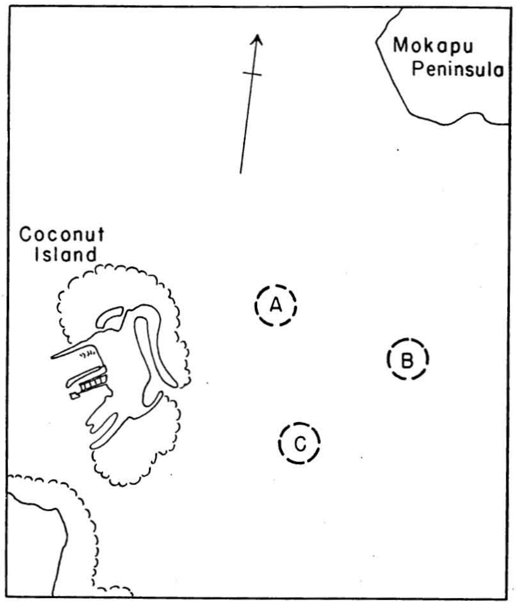

FIG. 2. Map showing the location of Substations A, B, and C at Station 4.

METHODS AND MATERIAL

Eggs and larvae were collected with specially constructed plankton nets having a mouth opening of 50 cm. and an overall length of 2 meters. They were modeled after the Hensen egg net, i.e., the diameter expanded to 75 cm. over a distance of 30 cm. back of the mouth, and then contracted in a cone with a 9 cm. diameter at the cod end. The forward expanding part was made of light canvas; the after conical part was made of No. 40 mesh, xxx grit gauze (aperture 0.47 mm.). An Atlas current meter was suspended in the center of the mouth by three wire supports equipped with turnbuckles. A cod end, also of No. 40 mesh grit gauze, 30 cm. in length and 9 cm. in diameter, was fastened to the end of the net by a detachable net band.

Sampling was confined to the vicinity of Station 4, located between Coconut Island and Mokapu Peninsula (Fig. 2) where as already indicated, previous work had shown a fairly consistent peak of abundance of nehu eggs (Tester, 1951: 336). Three substations (A, B, and C) were chosen at the apices of an equilateral triangle such that they were approximately 800 meters apart. Their positions were fixed by reference points on shore so that they could be located with reasonable precision on each trip.

Hauls were made twice a week, usually on Tuesday and Friday or on Monday and Thursday, starting August 31, 1950 and ending September 2, 1952. The sequence was interrupted only in two weeks when the "Salpa" was out of commission, and only one haul per week was made. On two occasions when the "Salpa" was in drydock, the hauls were made from a 24-foot plane personnel boat, but the methods and procedures were essentially similar to those used with the other vessel.

On each trip to Station 4, one 5-minute haul was made at each of the three substations, following a circular course with a diameter of about 300 meters. The circular rather than straight line course was chosen in order to keep the sampling within the presumed area of egg concentration and to avoid a bias associated with direction and distance of haul (Tester, 1951: 332).

Each haul was made in precisely the same manner. The current meter was read; the net was lowered over the side; the ship's speed was increased from 0 to about 2 to 3 knots so that the upper edge of the mouth of the net was towed about 15 cm. below the surface of the water at a distance of about 25 meters astern. During the first haul in each set of three, the temperature was read to the nearest tenth of a degree (C.) from a freshly-scooped bucket of sea water, and a sample of sea water was taken for later chlorinity determination in the laboratory. At the end of exactly five minutes, the ship was stopped, the net was hauled alongside by hand, the current meter was re-read, the net was thoroughly washed from the outside with a power hose, it was hauled aboard, the cod end was removed and the contents placed in a quart jar with the usual care in rinsing, washing, etc. The jar was then labelled and formalin was added to make a solution of approximately 10 per cent.

In the laboratory, the plankton was placed in Petri dishes, sorted by eye and by low power dissecting microscope, and all nehu eggs and larvae were removed and counted. The larvae were subsequently checked for correct indentification under higher magnification and were measured to the nearest 0.1 mm. from the tip of the closed lower jaw to the base of the tail, using an ocular micrometer. Chlorinity of the water samples (p.p.-m.) was determined by the Mohr method.

The Atlas current meters were standardized by determining the number of revolutions made in towing them at slow speed (about 3 knots—equivalent to about 3.7 revolutions per second) back and forth over a known distance between two buoys. There was close agreement between the calibration of the two meters, one of which was used for about 18 months and the other for the remaining 6 months. Calibration was undertaken but once rather than at intervals during the period of use. It is believed that this negligence led to no great error as (a) the meters were kept oiled, (b) the jewel bearings remained intact, and (c) there was no indication of a progressive change in the number of revolutions per 5-minute haul over the period of use.

As the hauls were standardized in time, the variation in volume of water strained from haul to haul was relatively small. Adjustment of the egg counts to a standard volume of water (100 cubic meters—a rough average of the actual volume strained per haul) was made, although it did not greatly alter the counts nor influence the major conclusions drawn from unadjusted data. The adjustments were made according to the following formula which is similar to that of Ahlstrom (1953: 6):

$$E_s = \frac{100\,E}{R.a.p.} = \frac{1{,}369.072\,E}{R}$$

where E_s is the number of eggs adjusted to a volume of 100 cubic meters of surface water;

E is the number of eggs per haul;

R is the number of revolutions of the meter per haul;

a is the area of cross-section of the mouth of the net (0.19635 square meters);

p is the length of the column of water needed to effect one revolution of the meter (0.372 meters).

The adjustment was not made for the larva count as the numbers involved were small and in most cases remained unchanged when the adjusted values were rounded to the nearest whole number. The unadjusted data may be considered to represent the number of larvae per 100 cubic meters of surface water.

RESULTS

Variation with Substation

Adjusted egg counts at Substations A, B, and C ranged respectively from 0 to 1,661, 0 to 1,722, and 0 to 2,617, with grand arithmetic means of 60.6, 61.8, and 81.1 eggs per 100 cubic meters for the 207 sampling days

TABLE 1
ANALYSIS OF VARIANCE OF (TRANSFORMED) EGG AND LARVA COUNT OVER A TWO YEAR PERIOD

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F
Egg Count:				
Substations	2	0.6248	0.3124*	3.2
Days	206	416.5646	2.0222**	21.0
Error	412	39.6087	0.0961	—
Larva Count:				
Substations	2	0.0184	0.0092	0.2
Days	206	65.9477	0.3201**	6.4
Error	412	20.5733	0.0499	—

* P about 0.05; ** P less than 0.01.

over the 2 year period. In the basic adjusted data, the range (and hence the standard deviation) of the substation determinations was obviously correlated with the mean, indicating the need for a transformation of the data in order to apply tests of significance. A logarithmic transformation was used: $y = \log(x + 1)$ (Barnes, 1952: 65); this not only tended to decorrelate the standard deviation and the mean but also avoided the logarithm of zero.

The transformed data were analyzed according to two criteria of classification, substations and days, with the results included in Table 1. There are highly significant differences between the three geometric means for substations: A–6.36, B–7.94, and C–8.80. Apparently on the average, Substation C was located closest to the focus of abundance of eggs in the southern sector of the bay (Tester, 1951: 336). The large and highly significant variation between sampling days was anticipated, and reflects both erratic daily egg production and seasonal variation in spawning activity.

Larva counts at Substations A, B, and C ranged respectively from 0 to 62, 0 to 51, and 0 to 57, with grand arithmetic means of 2.66, 2.18, and 2.44 larvae per 100 cubic meters. As shown in Table 1, there were no significant differences between the geometric means for substations (A–0.97, B–0.92, and C–0.98) but, as in the case of the eggs, there were highly significant differences between the means for days.

The great decline in numbers between the egg and larva stage is worthy of note and will be referred to again. For the grand arithmetic mean the decline is from 67.8 to 2.4 (96.5 per cent) and for the grand geometric mean it is from 7.01 to 0.96 (86.3 per cent.)

Variation with Time

The logarithms of the adjusted egg counts were averaged for each sampling day and were plotted against time (the detailed graph is not reproduced). It was at once apparent that there was considerable variation in mean egg count between successive sampling days during certain months. For example, on June 5, 8, and 12, 1951, the geometric mean counts per 100 cubic meters were respectively 10.2, 607.0, and 21.2; on July 2, 5, and 9, 1951, they were 0.8, 537.4, and 288.0. It is possible that this large daily variation in egg count could be due to shifting of the focus of spawning to and away from the vicinity of Station 4. However, it seems more likely that it is due mostly to large daily variation in actual egg production and thus in spawning activity. If so, it would be of interest to discover the cause or causes.

Perusal of the data on temperature and salinity indicated that these factors per se were not responsible for the variation in egg count between sampling days. It was apparent, without statistical analysis, that there was no significant relationship.

Attention was next directed to the possibility of lunar effects. On the basis of one series of samples taken in Ala Wai Canal during July, 1949, Tester and Yamashita (1950: 1) suggested that spawning activity might be related to the lunar cycle, with maximum spawning during the first quarter and minimum spawning during new moon. To investigate a possible lunar relationship, geometric means of the adjusted egg counts were calculated according to lunar days for the years 1950–51 and 1951–52. The data were then grouped according to phases of the moon. The geometric means for dark, first quarter, full, and third quarter were respectively 13.63, 18.20, 13.55, and 12.04 in 1950–51, and 4.53, 3.54, 2.61, and 2.66 in 1951–52. The differences in mean count between phases were neither statistically significant nor were they consistent during the two years. The present data yield no evidence of lunar periodicity in spawning. The cause or causes of the large variation between successive sampling days remains unknown.

Despite the large variation between successive sampling days it is evident from the data that spawning is seasonal in nature with a peak production of eggs during the summer months and a low production during the winter months. This is best illustrated by the geometric means per 100 cubic meters according to successive months as given in Table 2 and portrayed on a logarithmic ordinate scale in Figure 3A. Average production of eggs was highest during July, 1951, and next highest during August, 1952. It was relatively low during the winter months of 1950–51, and still lower during the winter months of 1951–52.

The seasonal march of egg production follows closely the seasonal march of temperature (Table 2), but this does not necessarily imply a dependent relationship. There is a marked difference in egg production between 1950–51 and 1951–52 (September to August, inclusive) with a geometric mean for the former of 14.12 and for the latter 3.27 eggs per 100 cubic meters. For the corresponding periods, mean water temperatures were 25.00° C. and 24.38° C. and mean chlorinities were 18.91 p.p.m. and 19.10 p.p.m., suggesting that higher temperatures and/or lower chlorinities were favorable for greater egg production. This possibility was investigated further using as variates the difference (with due regard to sign) between the means for the same months in the two years for temperature, chlorinity, and log egg count. Neither of the two partial regression coefficients (0.22 for log egg count and temperature; 0.06 for log egg count and chlorinity) was significant. The multiple correlation coefficient ($R = 0.41$) indicated that 83 per cent ($1-R^2$) of the total variation in egg count differences was unexplained by variation in the differences for temperature and chlorinity. It may be pointed out that this method of handling the data nullifies the seasonal trends. Although the results suggest that temperature may influence

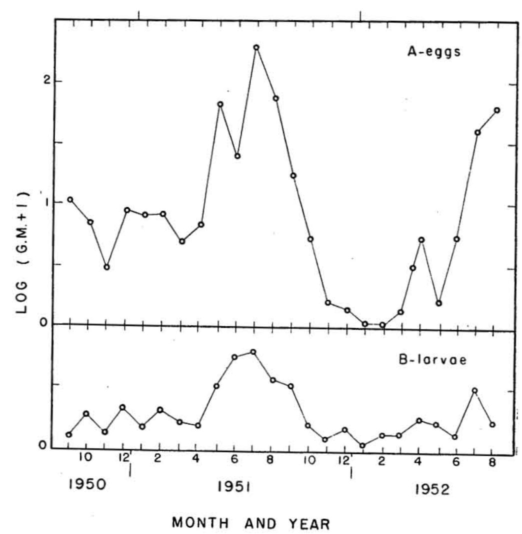

FIG. 3. Seasonal variation in the abundance (logarithm of the geometric mean plus one) of (A) eggs and (B) larvae.

TABLE 2
GEOMETRIC MEAN (G.M.) EGG AND LARVA COUNTS AND ARITHMETIC MEAN TEMPERATURES (°C.) AND CHLORINITIES (P.P.M.) ON A MONTHLY BASIS

MONTH AND YEAR	EGGS		LARVAE		TEMPERATURE	CHLORINITY
	Log (G.M. + 1)	G.M.	Log (G.M. + 1)	G.M.		
9/50	1.0223	9.53	0.1129	0.30	26.7	19.41
10/50	0.8504	6.09	0.2924	0.96	26.4	19.50
11/50	0.4855	2.06	0.1534	0.42	25.0	19.06
12/50	0.9485	7.88	0.3331	1.15	22.4	18.25
1/51	0.9234	7.38	0.1996	0.58	22.8	19.07
2/51	0.9289	7.49	0.3280	1.13	22.9	18.98
3/51	0.7028	4.04	0.2305	0.70	23.1	17.85
4/51	0.8264	5.70	0.1988	0.58	24.4	18.49
5/51	1.8148	64.30	0.5071	2.22	25.8	18.87
6/51	1.4007	24.20	0.7074	4.10	26.8	19.04
7/51	2.3013	199.10	0.7487	4.61	26.7	19.18
8/51	1.8714	73.40	0.5842	2.85	27.0	19.24
9/51	1.2416	16.40	0.5409	2.47	27.4	19.27
10/51	0.7202	4.25	0.2013	0.59	26.3	19.11
11/51	0.2159	0.64	0.0957	0.25	24.6	19.09
12/51	0.1403	0.38	0.1746	0.50	23.2	18.65
1/52	0.0334	0.08	0.0576	0.14	22.2	18.73
2/52	0.0251	0.06	0.1401	0.38	22.9	18.92
3/52	0.1453	0.40	0.1357	0.37	22.4	19.26
4/52	0.7286	4.35	0.2497	0.78	23.4	19.30
5/52	0.2177	0.65	0.2182	0.65	23.9	18.98
6/52	0.7278	4.34	0.1310	0.35	24.6	19.25
7/52	1.6201	40.70	0.5042	2.19	25.5	19.29
8/52	1.7984	61.87	0.2257	0.68	26.2	19.29

egg production, this cannot be established as a conclusion from the present data.

Figure 2B shows that the larva count also varies seasonally with a high production in the summer and a low production in the winter months. As might be expected, there is high correlation between the log mean monthly egg and larva counts (r = 0.818; P < 0.01).

Mortality

When the eggs were counted, they were segregated into three categories—"normal," "damaged," and "agglutinated"—according to criteria established by Tester (1951: 325–326). The damaged eggs, with the inner membrane ruptured and the embryo shattered, were assumed to have suffered mechanical injury during capture. It was suggested that the agglutinated eggs, in which the yolk and embryo had disintegrated into a whitish mass, may have been dead before capture.

The numbers and percentages of eggs in the three categories, segregated according to months, are shown in Table 3. From the gross data, the (weighted) percentages of normal, damaged, and agglutinated eggs are respectively 46.2, 32.2, and 21.6. These may be compared with similar data collected in 1949 and 1950—48.4, 47.1, and 4.5—recalculated

TABLE 3

NUMBER (IN PARENTHESES) AND PERCENTAGE OF NORMAL, DAMAGED, AND AGGLUTINATED EGGS BY MONTHS

MONTH AND YEAR	NORMAL	DAMAGED	AGGLUTINATED
9/50	(129) 43.4	(49) 16.5	(119) 40.1
10/50	(102) 43.6	(66) 28.2	(66) 28.2
11/50	(32) 30.2	(29) 27.4	(45) 42.4
12/50	(71) 14.1	(138) 27.4	(295) 58.5
1/51	(29) 6.1	(242) 51.1	(203) 42.8
2/51	(66) 13.7	(222) 46.3	(192) 40.0
3/51	(4) 2.8	(109) 76.2	(30) 21.0
4/51	(124) 43.2	(143) 49.8	(20) 7.0
5/51	(784) 23.9	(1,386) 42.3	(1,110) 33.8
6/51	(1,830) 41.6	(1,555) 35.3	(1,018) 23.1
7/51	(6,110) 47.7	(4,648) 36.3	(2,048) 16.0
8/51	(3,991) 64.9	(1,089) 17.7	(1,072) 17.4
9/51	(528) 43.1	(323) 26.4	(373) 30.5
10/51	(292) 77.4	(32) 8.5	(53) 14.1
11/51	(19) 61.2	(7) 22.7	(5) 16.1
12/51	(5) 33.3	(4) 26.7	(6) 40.0
1/52	(2) 66.7	(0) 0.0	(1) 33.3
2/52	(0) 0.0	(0) 0.0	(2) 100.0
3/52	(1) 5.6	(6) 27.7	(12) 66.7
4/52	(47) 24.5	(143) 74.5	(2) 1.0
5/52	(3) 6.2	(23) 48.0	(22) 45.8
6/52	(23) 12.0	(81) 42.2	(88) 45.8
7/52	(521) 37.3	(450) 32.3	(424) 30.4
8/52	(1,344) 64.7	(446) 21.5	(286) 13.8
All	(16,057) 46.2	(11,191) 32.2	(7,492) 21.6

from data discussed by Tester (1951: 338–340). The differences between investigations in the last two categories may be due, in part at least, to a change in interpretation of borderline cases of the "damaged" and "agglutinated" condition, although an effort was made to acquaint each of the several plankton sorters with the same objective criteria. The indications are that the number of agglutinated eggs averaged higher in 1950–53 than in 1949–50, but perhaps in a smaller ratio than that shown by the data (21.6 to 4.5, or 5 to 1). In any case, it is believed that the interpretation of the differences between "damaged" and "agglutinated" was reasonably consistent within the recent investigation.

The monthly percentages listed in Table 3 vary widely, but show a tendency for normal eggs to be relatively more abundant than agglutinated eggs during the summer and for agglutinated eggs to be relatively more abundant than normal eggs during the winter. The seasonal trend is illustrated in Figure 4. Because of the varying inherent accuracies of the percentages it is difficult to establish the statistical significance of the seasonal change. However, it may be shown readily that the differences in monthly ratios of normal to total and of agglutinated to total are unlikely due to chance. For example, a test of independence applied to the ratios of agglutinated to total yielded an extremely high Chi-square (3,067 for 21 degrees of freedom) which was highly significant ($P < 0.001$).

If the eggs classed as agglutinated were actually dead at the time of sampling, it would seem that this source of natural mortality was more pronounced in the winter, the period of small spawning, than in the summer, the period of large spawning. This suggests a further investigation of (1) the assumption that agglutinated eggs were dead at the time of sampling, and if this is established, (2) the causes of mortality of the eggs.

Reference may again be made to the grand geometric means for eggs and larvae (7.01 and 0.96 per 100 cubic meters) and to the great reduction in numbers (86.3 per cent). As the eggs hatch within 24 hours whereas the larvae persist in the catches for several days, the mean count for eggs would be expected to be smaller rather than larger than that of the larvae. There are several possible explanations for the relatively small mean larva counts:

(a) The larvae may be carried away from Station 4 by a slow clockwise current drift as suggested by Tester (1951: 342) following a study of variation in length distribution of the larvae.

(b) The thin filiform larvae, particularly after yolk sac absorption, may slip through the meshes of the net.

(c) The newly hatched larvae may sink below the surface layer which was sampled. Yamashita (MS: 14) has shown that in aquaria the newly hatched nehu larvae tend to sink. Although in simultaneous tows made by Tester (1951: 335) there was no significant evidence of more larvae at a depth than at the surface, the numbers caught were too few to warrant a conclusion.

(d) The newly or recently hatched larvae may suffer a high natural mortality. It seems idle to speculate further on this or other possibilities in view of the probable action of (a), (b), and perhaps (c), as outlined above.

Perusal of Table 2 will disclose that the ratio of egg to larva number varies considerably

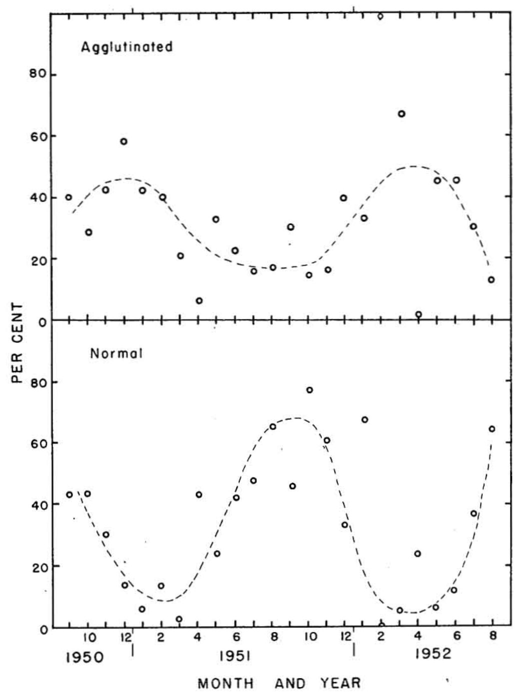

FIG. 4. Seasonal variation in the percentage of agglutinated and normal eggs.

from month to month. The most striking discrepance occurs in the months of December, January, and February, 1951–52, when the mean egg count is less, rather than greater, than the mean larva count. Although in these months the comparisons are intrinsically less reliable than in others because of the small numbers involved, nevertheless the discrepance seems due to factors other than chance. The reversal of the egg to larva ratio in the winter is contrary to what would be expected from the tendency, just discussed, for the percentage of agglutinated and presumably dead eggs to be higher in the winter than the summer: this should increase rather than decrease the winter egg to larva ratio. One possible explanation of the reversal is that in the winter of 1951–52 spawning of relatively small extent took place elsewhere than at Station 4, and that the larvae drifted into the sampling area.

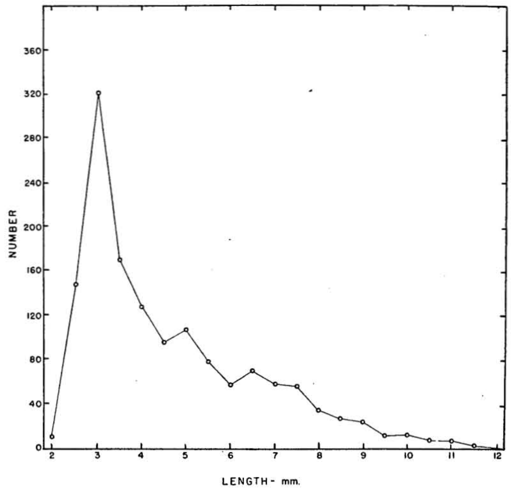

FIG. 5. Length frequency distribution of larvae.

Length Distribution of the Larvae

The nehu larvae ranged in length from about 2 to 11 mm. It is presumed that larger larvae were able to escape the net. It was hoped that the progeny of pulses of spawning could be followed by the progression of modes in the length distribution of successive samples of larvae. This was not possible because (a) the larvae were apparently dispersed from the sampling station too rapidly and (b) the samples were not taken at sufficiently close time intervals.

The composite length distribution of all larvae sampled at Station 4 is shown in Figure 5. It is similar to that shown by Tester (1951: fig. 6) in that a main mode appears at 3 mm. and less pronounced modes appear at greater lengths. The latter differ slightly in position from those reported earlier but this may be attributed to the fact that sampling was confined to one station in the present investigation and therefore did not adequately sample the larger larvae which drifted elsewhere. The minor modes are presumed to be real and to be related to the presence of "day groups." As in the previous investigation (Tester, 1951: 341), they suggest an average early growth rate of about 1.5 mm. per day.

SUMMARY AND CONCLUSIONS

1. Quantitative samples of nehu eggs and larvae were taken in replicate twice a week over a two year period at one station in Kaneohe Bay, using a half-meter plankton net. The station was located at or near a focus of abundance of eggs in the southern sector of the bay.

2. Spawning, as indicated by egg and larva catch, occurred erratically throughout the year, but with a summer maximum and a winter minimum.

3. Variation in egg production between days could not be adequately explained by variation in temperature, chlorinity, or moon phase.

4. Agglutinated eggs, with the embryo and yolk coagulated beyond recognition, formed a higher percentage than in a previous investigation. Moreover in the present material, the percentage was higher in winter than in summer. The suggestion that agglutinated eggs were dead at the time of capture should be investigated further.

5. Several possible explanations are advanced for a large decrease in numbers between the egg and larva stage, namely, drift of larvae from the sampling station, escape through the meshes of the net, sinking below the surface layers, and loss from mortality. A seasonally erratic egg to larva ratio is pointed out.

6. The sampling is not adequate to trace pulses of spawning from the egg to the larva stages. A length frequency distribution of the larvae is included showing the presence of one major and several minor modes similar to those found in a previous investigation.

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